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A review of *Willemia buddenbrocki*-group (Collembola, Poduromorpha, Hypogastruridae) with cladistic analysis

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The authors describe three new species of Collembola belonging to the genus *Willemia*, one found in Thailand and New Caledonia, and the other two in Nepal. Redescriptions of *W. nadchatrami* Yosii, 1959 and *W. brevispina* Hüther, 1962 are proposed. A comparative table of species from the *Willemia buddenbrocki*-group is given, as well as an identification key to this monophyletic group. A cladistic analysis of this group is performed with Hennig86.

KEYWORDS: *Willemia*, Hypogastruridae, Collembola, identification key, phylogeny.

Introduction

In 1901, Börner created the genus *Willemia* with the type species *Willemia anophthalma*. At present this genus includes 33 species. It has a worldwide distribution, represented by euedaphic species living in the fairly humid zone of the soil (Ponge, 1980; Ponge and Prat, 1982), and in the interstitial littoral sand (Thibaud and Massoud, 1988; Thibaud and Lee, 1994; Thibaud and Christian, 1995; Najt and Weiner, 1997; Thibaud and Weiner, 1997), where the density is rather low.

The present work considers the species of the genus *Willemia*, of *W. buddenbrocki*-group, characterized by large *e3* and *i2* sensilla placed in cavities and covered in part by a tegumental fold. They share three other characters: the presence of six setae on antennal segment I, 11 setae on antennal segment II, and the absence of seta *a0* on the head. Previously, this group contained nine species. In 1959 Hüther described the first species with these characters, *Willemia buddenbrocki*, from a vineyard near Edsheim in Germany. Later, in 1962, he described a new subspecies *W. buddenbrocki brevispina* from different forests in El Salvador, which is now considered a separate species. *W. australis* Rapoport, 1962 was described from Bahia Blanca Province, in salpetrous marsh in Grünbein (Rapoport, 1962). Two other species were described by Prabhoo (1971): *W. delamarei* and *W. setonychia*, both from a tea plantation in Kerala, India. In 1959, Yosii described *W. nadchatrami* from Batu Cave in Malaysia. *W. neocaledonica* Weiner, 1991 is known from Cyperaceae turf in New Caledonia. In 1992, Christiansen and Bellinger described *W. peke* from soil under grass in sugarcane fields, in Hawaii. *W. wandae* Tamura,

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1997 was described from a tropical rain forest in Mengla, Yunnan Province, Southwest China (Tamura and Zhao, 1997). We present below descriptions of three new species (*W. deharvengi*, *W. annapurna* and *W. nepalensis*); a redescription of *W. brevispina*, with its new synonyms (*W. australis* Rapoport, 1962 and *W. peke* Christiansen and Bellinger, 1992); redescription of *W. nadchatrami*; and some remarks concerning *W. wandae* and *W. neocaledonica* with new locality information.

Abbreviations: MNHN, Laboratoire d'Entomologie, Muséum national d'Histoire naturelle, Paris; ISEA, Institute of Systematics and Evolution of Animals, Polish Academy of Sciences, Kraków.

Systematic account

Willemia deharvengi sp. n.
(Figures 1–12, table 1)

Material

HOLOTYPE: ♀, Thailand, Chiang Mai Province, Doi Inthanon (way of Mae Chaem); dry secondary forest, in soil, 1150 m a. s. l.; 30.vi.1991, L. Deharveng and A. Bedos (MNHN); PARATYPES: 2 ♀♀, same data as the holotype (MNHN and ISEA); New Caledonia, beach of Thio, fine, black sand, *Hypomea*, 15.i.1995, J.-M. Thibaud, four specimens; beach of Maamaat-Balade, 8 km northeast of Poubeo, yellow, semi-fine sand, 18.i.1995, J.-M. Thibaud, one specimen; Lifou Island: beach of Easox, 6 km west of Xepenhe, 21.i.1995, J.-M. Thibaud, one specimen.

Description

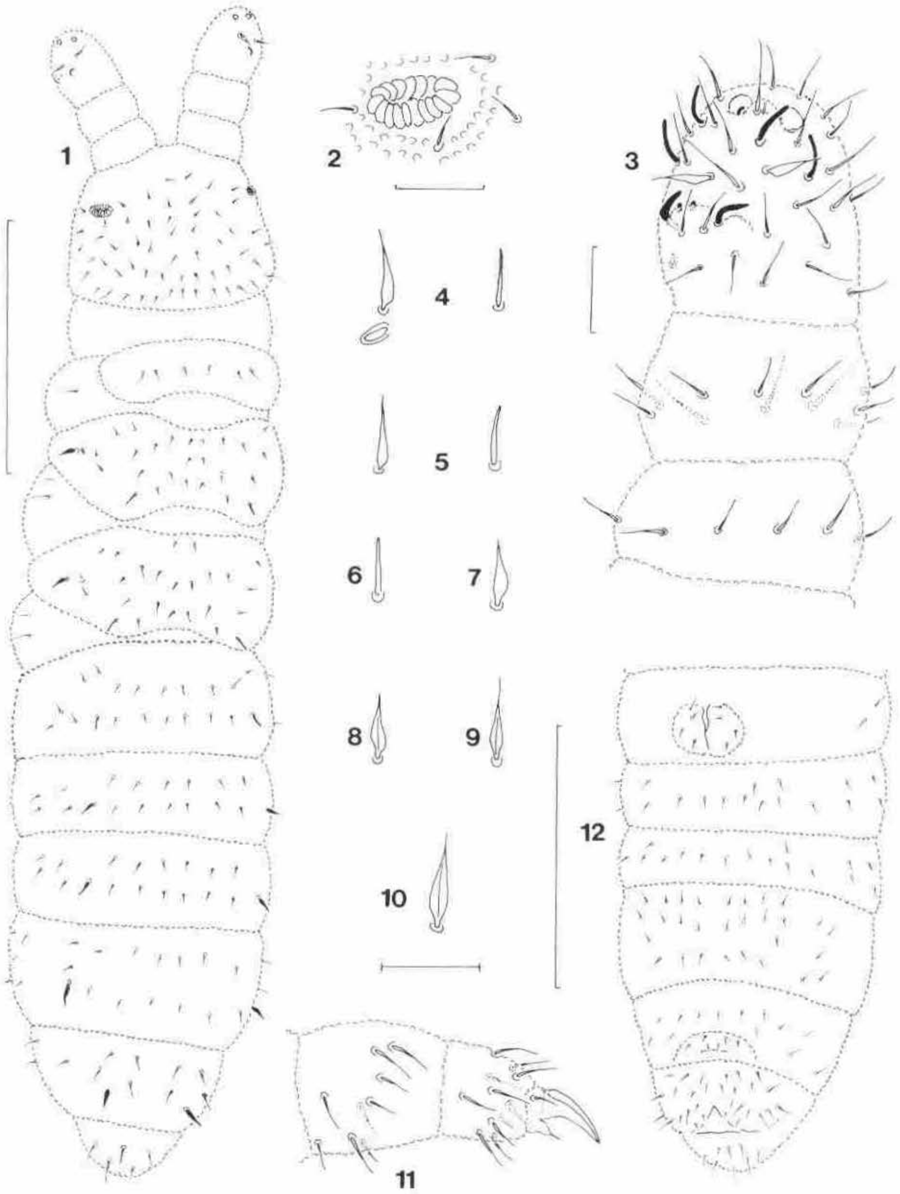
Female (holotype) length 0·40 mm, paratypes (females) length 0·35 mm and 0·49 mm. Colour in alcohol white, tegumental granulation normal.

Antennae somewhat shorter than head's diagonal. Antennal segments III and IV only slightly divided. Antennal segment I with six setae, antennal segment II with 11 setae. Sensory organ of antennal segment III consisting of two small internal sensilla hidden behind a tegumental fold, two guard sensilla curved in same direction, and one ventrolateral microsensillum. Guard setae longer than or subequal to guard sensilla. Antennal segment IV with four subcylindrical sensilla (*e1*, *e2*, *i1* and *d*), two large globular sensilla *e3* and *i2*, each one in a cavity, not covered by tegumental fold, external cavity with microsensillum, two lanceolate setae, subapical organite present between globular sensilla. Apical vesicle absent (figure 3).

Postantennal organ with 16–17 vesicles (figure 2). Setae *c1* present on the head. Mouth parts relatively well developed. Labrum with 2/534 setae.

Dorsal chaetotaxy presented in figure 1. Half tergite formula of setae *s*: 2, 2/1, 1, 1, 1, 1 in *m7* and *p4* position on thoracic tergites II and III, in *p4* position on abdominal tergites I–IV, and in *p2* position on the abdominal tergite V. Setae *s* lanceolate except $s=p4$ on second and third thoracic tergite and first abdominal tergite, which are subcylindric with acuminate apex (figures 4–10). Microsensilla *ms* on thorax II. Setae *m3* absent on abdominal tergite IV, setae *a3* present on abdominal sternites II and IV. Ventral chaetotaxy as in figure 12; setae *a3* on abdominal sternite II present. Ventral tube with 4+4 distal setae.

Tibiotarsus I, II and III with 12, 12 and 11 setae respectively, without tenent



FIGS 1–12. *Willemia deharvengi* sp. n.: (1) dorsal chaetotaxy (scale 0·1 mm); (2) postantennal organ (scale 0·01 mm); (3) antennal segment I, II, III and IV (scale 0·01 mm), (4) seta *s* and microsensillum *ms* of thorax II (scale 0·01 mm); (5) seta *s* of thorax III (scale 0·01 mm); (6) seta *s* of abdomen I (scale 0·01 mm); (7) seta *s* of abdomen II (scale 0·01 mm); (8) seta *s* of abdomen III (scale 0·01 mm); (9) seta *s* of abdomen IV (scale 0·01 mm); (10) seta *s* of abdomen V (scale 0·01 mm); (11) tibiotarsus III (scale 0·01 mm); (12) ventral abdominal chaetotaxy of the female (0·1 mm).

hair. Claw curved, toothless. Empodial appendage as long as 0·33 of the length of inner edge of claw, distally setaceous (figure 11).

Anal spines absent.

Table 1. Characters differentiating species of the *W. buddenbrocki*-group.

	Willemia annapurna	*Willemia brevispina*	*Willemia buddenbrocki*	*Willemia deharvengi*	*Willemia delamarei*	*Willemia nadchatrami*	*Willemia neocaledonica*	*Willemia nepalensis*	*Willemia setonychia*	*Willemia wandae*
Apical vesicle on ant. IV	present	present	present	absent	present	present	present	present	absent	present
Subcyldrincal sensilla on ant. IV	4	2	4	4	4	4	4	4	4	4
Lanceolate setae on ant. IV	0	0	0	2	0	0	0	0	0	0
Guard setae/guard sensilla	≥	≥	>	≥	≥	>	<	≥	>	≥
Vesicles number in PAO	19–21	7–10	12–13	15–17	8–12	8–9	10–15	14–15	18–20	13–14
Shape of *e3* and *i2* sensilla	globular	globular	globular	globular	globular	'francisque'	globular	globular	globular	globular
c1 setae on the head	present	absent	absent	present	present	absent	absent	present	present	absent
Curved and crenated setae	absent	absent	absent	absent	absent	present	absent	absent	absent	absent
Setae number on thorax I	6	6	6	6	6	4	6	6	6	6
Setae *s*=*m7* on thorax III	sub-cylindrical	sub-cylindrical	sub-cylindrical	lanceolate	lanceolate	sub-cylindrical	sub-cylindrical	lanceolate	lanceolate	lanceolate
Setae *s* on abdominal tergites IV and V	sub-cylindrical	sub-cylindrical	sub-cylindrical	lanceolate	lanceolate	sub-cylindrical	sub-cylindrical	sub-cylindrical	lanceolate	sub-cylindrical
Setae *s* position on abdominal tergite V	*p2*	*p2*	*p2*	*p2*	*p2*	*p3*	*p2*	*p2*	*p2*	*p2*
Setae number on tibiotarsi I and II	11	12	11	12	?	12	12	12	?	11
Setae number on tibiotarsus III	10	12	11	11	?	12	12	12	?	11
a3 setae on abdominal sternit II	present	absent	present	present	?	absent	absent	present	?	absent
a3 setae on abdominal sternit IV	present	present	present	present	?	present	present	present	?	absent
m1 setae on abdominal sternit IV	present	present	present	present	?	absent	present	present	?	present
Ratio claw III : anal spine	1:0·9	1:0·8	1:1·2	anal spines absent	1:0·7	1:0·9	1:1	1:0·7	anal spines absent	1:1·3

Discussion

The new species is exceptional among all the species of the *W. buddenbrocki*-group because of the presence of two lanceolate setae on antennal segment IV, which in the specimens from New Caledonia are not so distinct as in specimens from Thailand. These specimens have 15–16 vesicles in postantennal organ, while the specimens from the type locality have 16–17 vesicles. This species shares with *W. setonychia* the absence of anal spines and absence of apical vesicle. They differ in the number of vesicles in the postantennal organ (15–17 in *W. deharvengi*, 18–20 in *W. setonychia*).

Etymology

This new species is cordially dedicated to our colleague and friend, Louis Deharveng.

Willemia brevispina Hüther, 1962

= *Willemia australis* Rapoport, 1962 syn. nov.
= *Willemia peke* Christiansen and Bellinger, 1992 syn. nov.
(Figures 13–24, table 1)

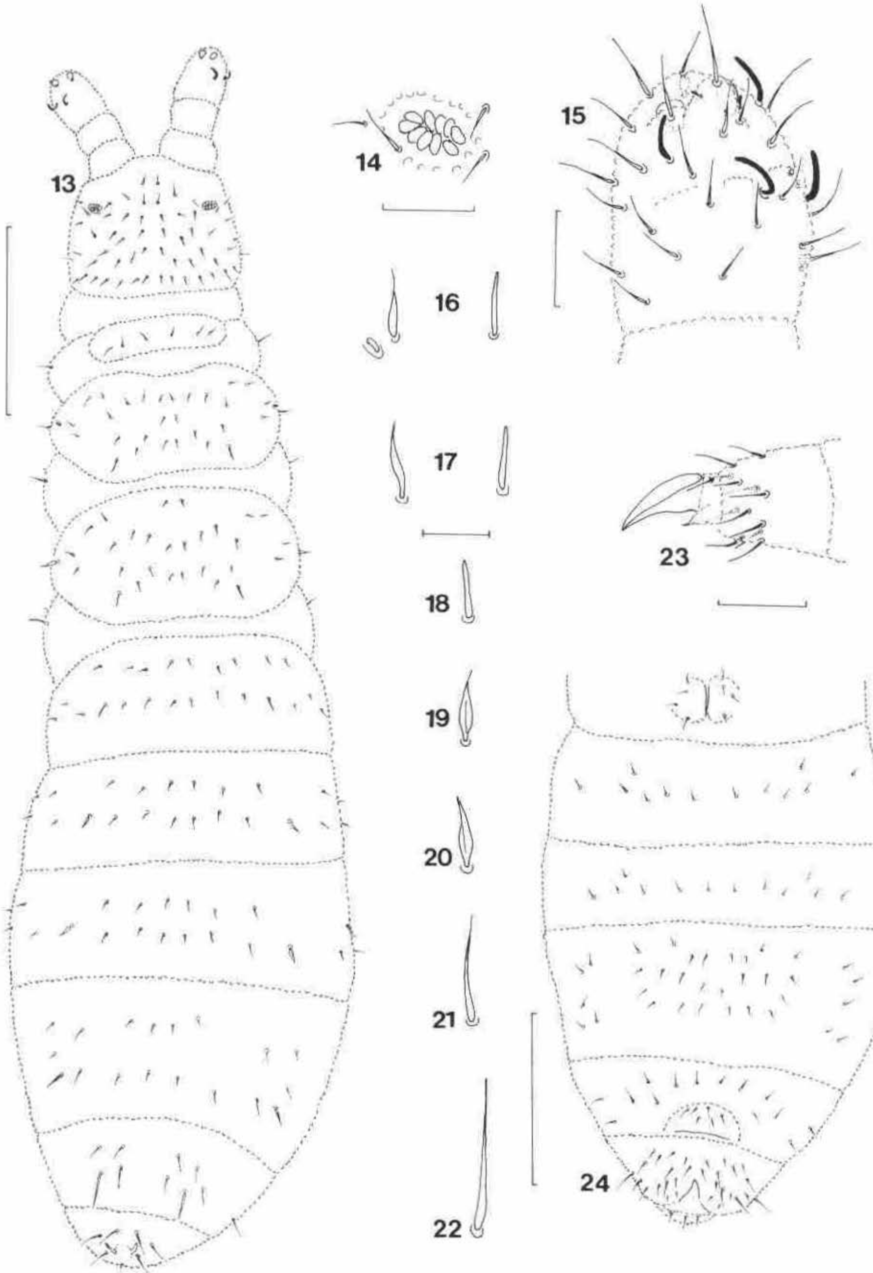
Material

Mexico, Jalisco, Chamela, litter, 13.x.1991, A. Rodríguez and J. A. Gómez, one specimen; Mexico, Jalisco, Chamela, litter, 16.xi.1991; A. Rodríguez and J. A. Gómez, one specimen; Mexico, Mapimi, Durango, rat nest in a dune, 13.vi.1985, J. Palacios-Vargas and J. Najt, three specimens; Guadeloupe, Grande-Terre, sand, beach, near Anse du Mont, 5.xi.1987, J.-M. Thibaud, two specimens; Guadeloupe, Grande Terre, sand beach Anse Laborde, 6.xi.1987, J.-M. Thibaud, one specimen; Guadeloupe, Marie-Galante, sand beach in front of Murat castel, 11.xi.1987, J.-M. Thibaud, one specimen; Martinique, sand beach of Cap Chevalier, 25.v.1989, J.-M. Thibaud, one specimen; Martinique, sand, beach les Salines, 20.v.1989, J.-M. Thibaud, two specimens; Thailand, Kanchanaburi Province, Suphan Buri, mouth of the Cave Tham Nam, soil, 23.vi.1987, L. Deharveng and A. Bedos, one specimen; Hawaii, Oahu: Weed Circle near Waialua, soil under grass, 28.x.1966, K. Christiansen and P. Bellinger (PB (4812) Bernice P. Bishop Museum, Honolulu, Hawaii), two females; Argentina, Santa Cruz: aerodromo de Piedrabuena, 19.xi.1963, E. H. Rapoport, one specimen.

Redescription

Length 0·35–0·55 mm. Colour in alcohol white, tegumental granulation intermediate.

Antennae somewhat shorter than head's diagonal. Antennal segments III and IV slightly divided. Antennal segment I with six setae, antennal segment II with 11 setae. Sensory organ of antennal segment III consisting of two small internal sensilla hidden behind a tegumental fold, two guard sensilla curved in same direction, and one ventral microsensillum. Guard setae longer than or equal to guard sensilla. Antennal segment IV with two thick sensilla (*e2* and *i1*), thicker than ordinary setae; two large sensilla *e3* and *i2* pearshaped in lateral view, each one in a cavity, partially covered by tegumental fold, external cavity with a microsensillum, subapical organite present near to sensillum *e3*. Apical vesicle simple and globular (figure 15).



FIGS 13–24. *Willemia brevispina* Hüther, 1962: (13) dorsal chaetotaxy (0·1 mm); (14) postantennal organ (scale 0·01 mm); (15) antennal segment III and IV (scale 0·01 mm); (16) seta *s* and microsensillum *ms* of thorax II (0·01 mm); (17) seta *s* of thorax III (0·01 mm); (18) seta *s* of abdomen I (0·01 mm); (19) seta *s* of abdomen II (scale 0·01 mm); (20) seta *s* of abdomen III (scale 0·01 mm); (21) seta *s* of abdomen IV (scale 0·01 mm); (22) seta *s* of abdomen V (scale 0·01 mm); (23) tibiotarsus III (scale 0·01 mm); (24) ventral abdominal chaetotaxy of the female (scale 0·1 mm).

Postantennal organ with 7–10 vesicles (figure 14). Setae *c1* absent of the head. Mouth parts relatively well developed. Labrum with 2/534 setae.

Dorsal chaetotaxy presented in figure 13. Head without *a0* and *c1* setae. Half tergite formula of setae *s*: 2, 2/1, 1, 1, 1, 1 in *m7* and *p4* position on thoracic tergites II and III, in *p4* position on abdominal tergites I–IV, in *p2* position on the abdominal tergite V. Setae *s* lanceolate on second and third abdominal tergites (figures 16–22). Microsensilla *ms* on thorax II. Ventral chaetotaxy as in figure 24. Setae *a3* on abdominal sternite II absent, setae *a3* on abdominal sternite IV present. Ventral tube with 4+4 distal setae.

Tibiotarsus I, II and III with 12 setae each, without tenent hair. Claw curved, toothless. Minute empodial appendage, distally setaceous (figure 23).

Small anal spines curved. Ratio claw : anal spines = 1 : 0·8.

Discussion

Christiansen and Bellinger in 1992 described *Willemia peke* from Hawaii. After examination of the holotype and paratype, as well as the rich material of *W. brevispina*, we established that *W. peke* is a new synonym of *W. brevispina*. *Willemia australis* described by Rapoport in 1962 is also a new synonym of *W. brevispina*. They possess all the same characters.

This species can be distinguished from the others in the *buddenbrocki*-group by the *e1* and *d* setae on antennal segment IV not distinct from the ordinary setae.

Willemia nadchatrami Yosii, 1959

(Figures 25–32, table 1)

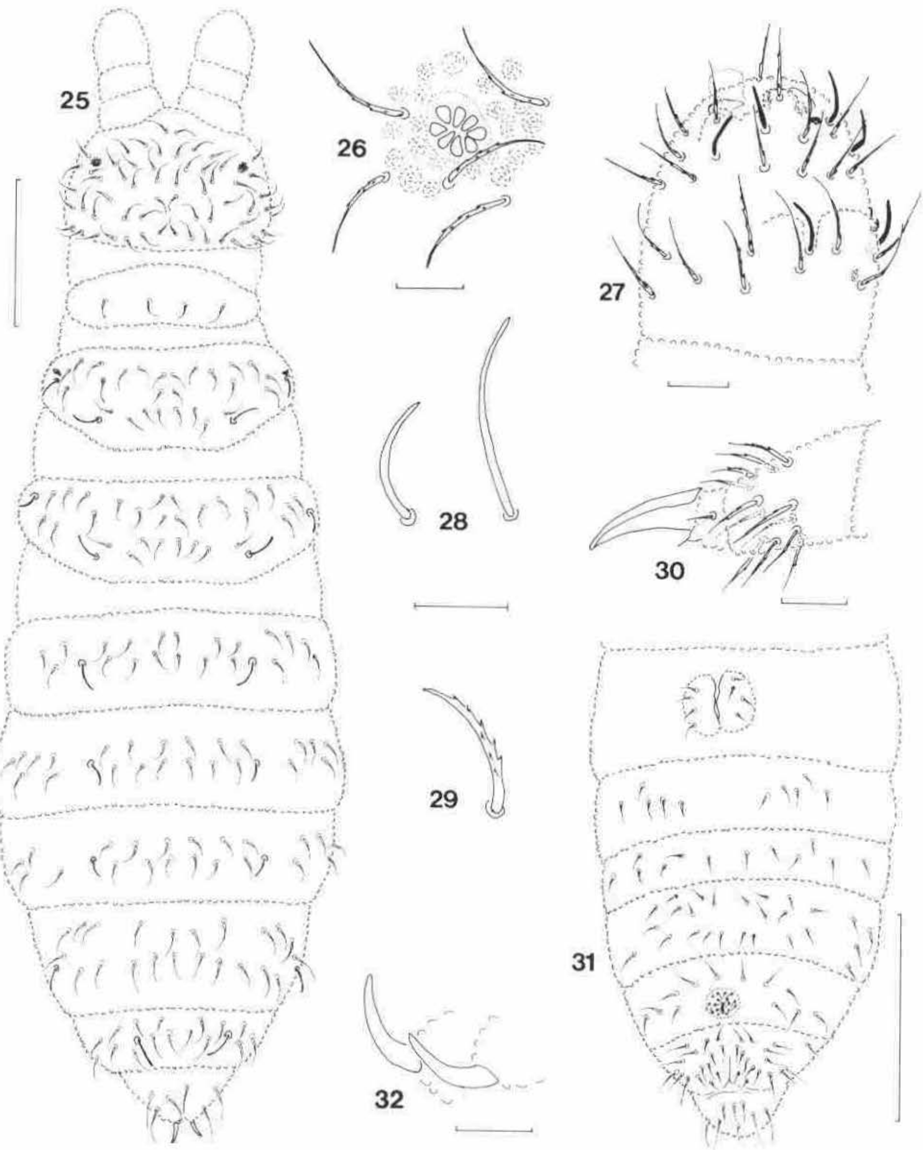
Material

Thailand, Phangna Province, Tham Poung Chang Cave, guano, 12.vi.1986, L. Deharveng and A. Bedos, four specimens; Thap Put, Tham Nam Cave, 20.vii.1987, P. Leclerc, one specimen; Surat Thani Province, Phanom, Tham Khao Phang Cave, 23.vii.1987, L. Deharveng and A. Bedos, one specimen; Surat Thani Province, Ban Sok, Tham Khao Sok Cave, litter and guano, 25.vii.1987, L. Deharveng and A. Bedos, one specimen; Yala Province, Ban Na Tham, Tham Sua Cave, 13.vii.1987, P. Leclerc, one specimen.

Redescription

Length 0·64–0·78 mm. Colour in alcohol white, tegumental granulation very strong, on abdominal tergite VI verrucous. Hypodermic reticulation clearly visible especially on the dorsal side of head and thorax.

Antennae shorter than head's diagonal. Antennal segments III and IV slightly divided. Antennal segment I with six setae, antennal segment II with 11 setae. Sensory organ of antennal segment III consisting of two small internal sensilla, both hidden behind a tegumental fold, two guard sensilla curved in the same direction, and one ventral microsensillum. Guard setae longer than guard sensilla. Antennal segment IV with four sensilla (*e1*, *e2*, *i1* and *d*), thicker than ordinary setae; two large sensilla *e3* and *i2* in the form of 'francisque' (flattened on the top), each one in a cavity, covered by a tegumental fold. External cavity with a microsensillum. Subapical organite between sensilla *e3* and *i2*, also covered by tegumental fold, globular apical vesicle. Setae of antennae serrated (figure 27).



FIGS 25–32. *Willemia nadchatrami* Yosii, 1959: (25) dorsal chaetotaxy (scale 0·1 mm); (26) postantennal organ (scale 0·01 mm); (27) antennal segment II, III and IV (scale 0·01 mm); (28) seta *s* and microsensillum *ms* of thorax II (scale 0·01 mm); (29) ordinary seta of thorax II (scale 0·01 mm); (30) tibiotarsus III (scale 0·01 mm); (31) ventral abdominal chaetotaxy of the male (scale 0·1 mm); (32) anal spines (scale 0·01 mm).

Circular postantennal organ with 8–9 vesicles (figure 26). Setae *c1* absent of the head. Mouthparts relatively well-developed. Labrum with 2/534 setae.

Dorsal chaetotaxy presented in figure 25. Dorsal setae curved and serrated (figure 29). Head without setae *a0* and *c1*. Thoracic tergite I with 2 + 2 setae, thoracic tergite II with microsensilla *ms*. Abdominal tergite IV with 5 + 5 setae in *a*-row and 6 + 6 setae in *p*-row. Some asymmetry in dosral chaetotaxy. Sensory setae *s* slightly differentiated: smooth and more transparent than normal setae. Half tergite formula of setae *s*: 2, 2/1, 1, 1, 1, 1 in *m7* and *p4* position on thoracic tergites II and III (figure 28), in *p4* position on abdominal tergites I–III, in position *p6* on abdominal tergite IV, in *p3* position on the abdominal tergite V. Ventral chaetotaxy as in figure 31, with smooth and straight setae; setae *a3* on second abdominal sternite absent and setae *m1* on abdominal sternite IV absent. Ventral tube with 4+4 distal setae.

Tibiotarsi I, II and III with 12 setae each, without tenent hair. Claw curved, toothless. Tiny empodial appendage, distally setaceous (figure 30).

Anal spines curved, ratio of claw III : anal spines = 1 : 0·9.

Discussion

Willemia nadchatrami Yosii, 1959 was described from Batu Cave in the Malayan Peninsula. The material, which was a basis of the redescription was collected in different caves in Thailand, and on the Malayan Peninsula. *W. nadchatrami* is exceptional among all species of *W. buddenbrocki*-group because of dorsal setae type, which are curved and serrated; strong tegumental granulation and hypodermic reticulation on the dorsal side of the body; presence of only 2+2 setae on thoracic tergite I (3+3 in the other species of the genus); and by absence of *m1* setae on abdominal sternite IV.

Willemia annapurna sp. n.

(Figures 33–44, table 1)

Material

Holotype: ♀, Nepal, Annapurna massif, Chame-Tarapani; deciduous forest, in humus, 2450 m; 4.x.1977, L. Deharveng (MNHN); Paratype: ♀, same data as holotype (ISEA); Nepal, Gosain Kund massif, central Nepal, near the Trisuli river, damp ripicolous forest with *Abies*, undergrowth with ferns, in humus, 2130 m; 22.xi.1978, P. Cassagnau, one specimen.

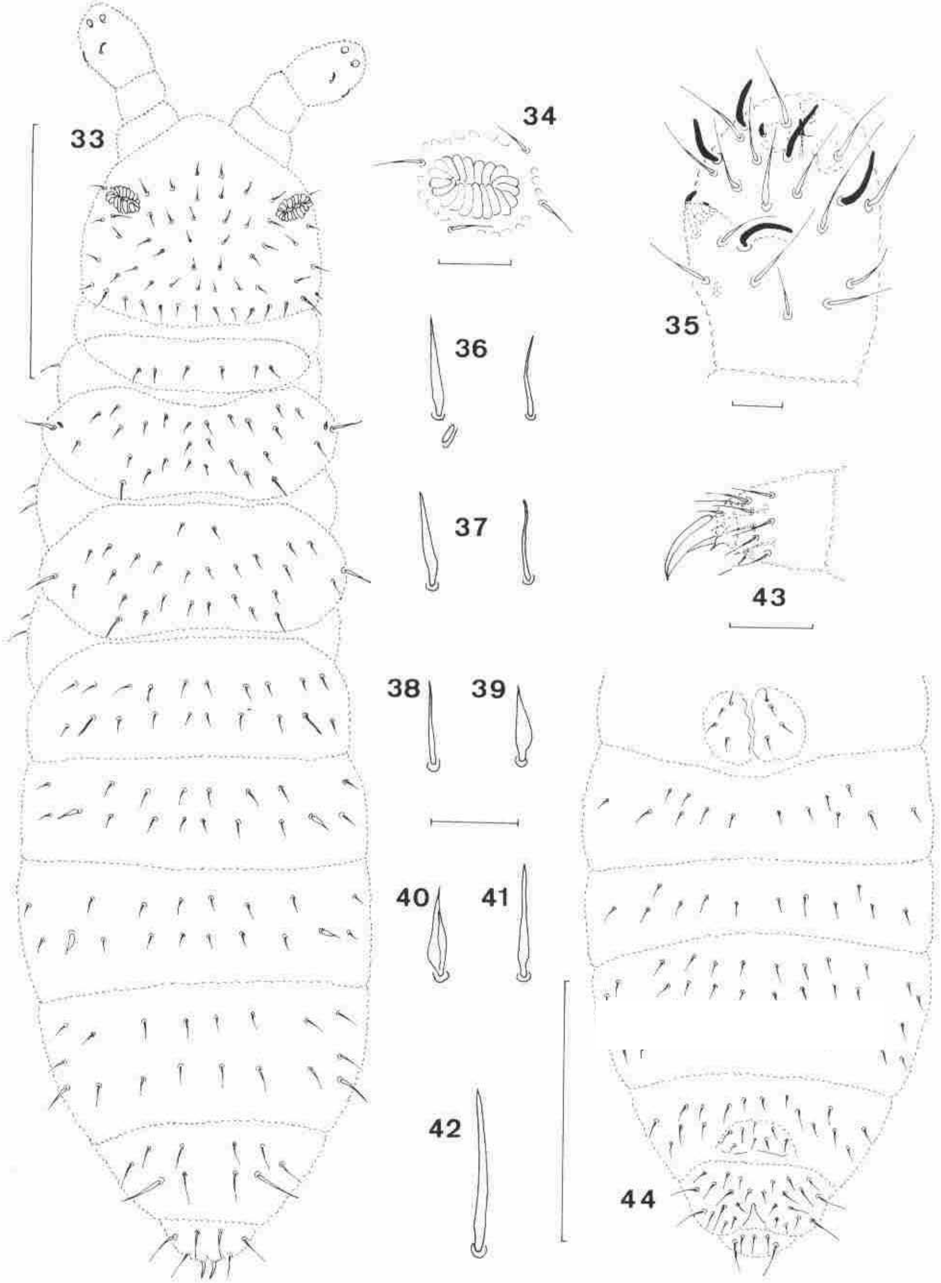
Description

Female (holotype) length 0·45 mm, paratype (female) length 0·36 mm. Tegumental granulation normal.

Antennae somewhat shorter than head's diagonal. Antennal segments III and IV only slightly divided. Antennal segment I with six setae, antennal segment II with 11 setae. Sensory organ of antennal segment III consisting of two small internal sensilla hidden behind a tegumental fold, two guard sensilla curved in same direction, and one ventrolateral microsensillum. Guard sensilla shorter than or equal to guard setae. Antennal segment IV with four subcylindrical sensilla (*e1*, *e2*, *i1* and *d*), two large globular sensilla *e3* and *i2*, each one in a cavity, covered by tegumental fold, external cavity with microsensillum, subapical organite present between globular sensilla. Apical vesicle simple and globular (figure 35).

Postantennal organ with 19–21 vesicles (figure 34). Setae *c1* present on the head. Mouthparts relatively well-developed. Labrum with 2/534 setae.

Dorsal chaetotaxy presented in figure 33. Half tergite formula of setae *s*: 2, 2/1, 1, 1, 1, 1 in *m7* and *p4* position on thoracic tergites II and III, in *p4* position on abdominal tergites I–IV, and in *p2* position on abdominal tergite V. Setae *s* lanceolate on the second and third abdominal tergites, microsensilla *ms* on thorax II (figures



FIGS 33–44. *Willemia annapurna* sp. n.: (33) dorsal chaetotaxy (scale 0·1 mm); (34) postantennal organ (scale 0·01 mm); (35) antennal segment III and IV (scale 0·01 mm); (36) seta *s* and microsensillum *ms* of thorax II (scale 0·01 mm); (37) seta *s* of thorax III (scale 0·01 mm); (38) seta *s* of abdomen I (scale 0·01 mm); (39) seta *s* of abdomen II (scale 0·01 mm); (40) seta *s* of abdomen III (scale 0·01 mm); (41) seta *s* of abdomen IV (scale 0·01 mm); (42) seta *s* of abdomen V (scale 0·01 mm); (43) tibiotarsus II (scale 0·01 mm); (44) ventral abdominal chaetotaxy of the female (scale 0·1 mm).

36–42). Setae *m3* absent on abdominal tergite IV. Ventral chaetotaxy as in figure 44; setae *a3* on abdominal sternite II present. Ventral tube with 4+4 distal setae.

Tibiotarsus I, II and III with 11, 11 and 10 setae respectively, without tenent hair. Claw curved, toothless. Empodial appendage present (figure 43).

Anal spines strong and curved, ratio claw III : anal spines = 1 : 0·9.

Discussion

The new species is very close to *Willemia buddenbrocki*, from which it differs mainly by number of vesicles in postantennal organ (12–13 in *W. buddenbrocki* and 19–21 in *W. annapurna*) and by presence of the setae *c1* on the head in the new species. It differs from all the other species by having 10 setae on third tibiotarsi.

W. annapurna is also close to *W. nepalensis* (see discussion on *W. nepalensis*).

Etymology

The species is named after type locality.

Willemia nepalensis sp. n.

(Figures 45–56, table 1)

Material

HOLOTYPE: ♀, Nepal Jaljale crest, north of Dankuta, oriental Nepal, Rhododendron forest, in moss on the ground, 2935 m, 6.xi.1978, P. Cassagnau (MNHN); paratypes: three specimens, same data as holotype (MNHN and ISEA).

Description

Female (holotype) length 0·47 mm, paratypes length 0·47–0·36 mm. Tegumental granulation normal.

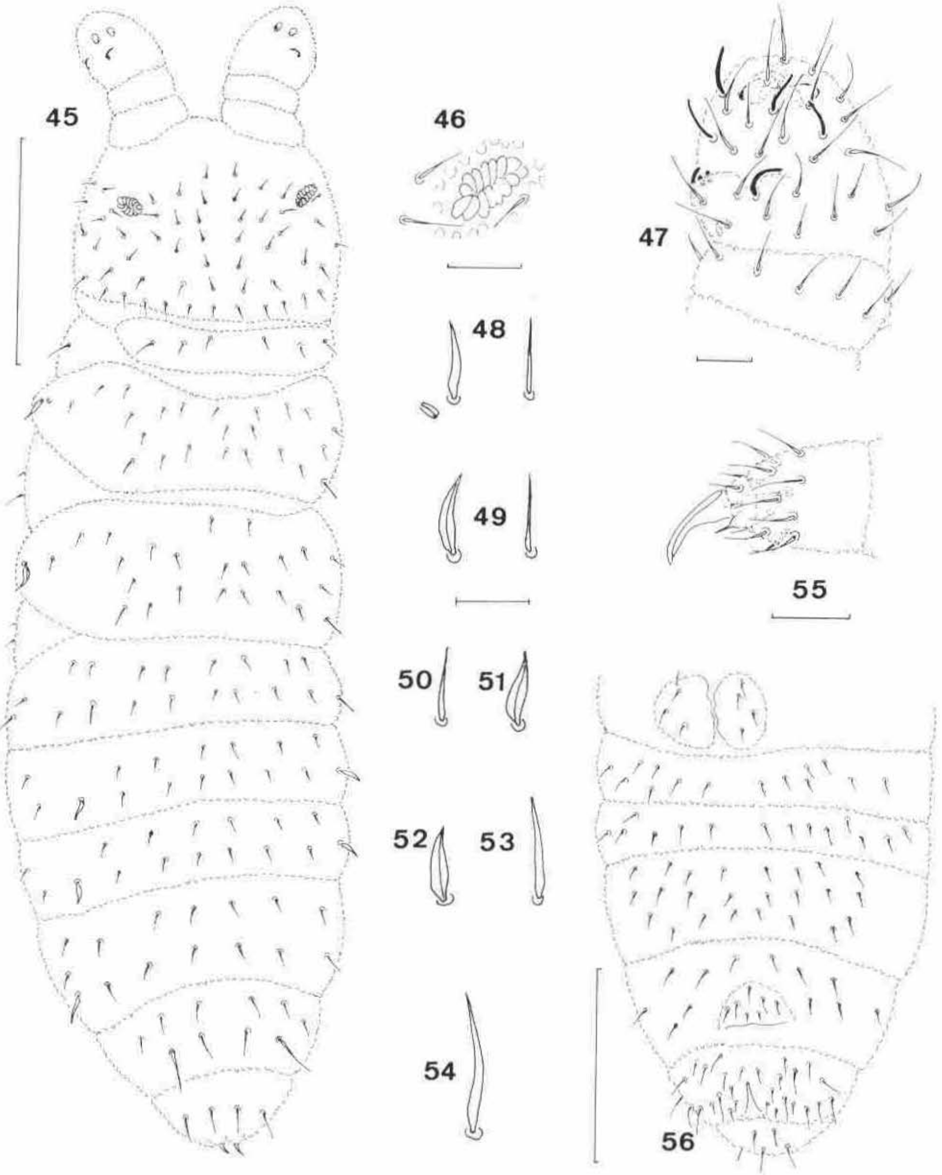
Antennae shorter than head's diagonal. Antennal segments III and IV slightly divided. Antennal segment I with six setae, antennal segment II with 11 setae. Sensory organ of antennal segment III consisting of two small internal sensilla hidden behind a tegumental fold, two guard sensilla curved in same direction, and one ventrolateral microsensillum. Guard setae longer than or equal to guard sensilla. Antennal segment IV with four subcylindrical sensilla (*e1*, *e2*, *i1* and *d*) hardly distinguishable from normal setae, two large globular sensilla *e3* and *i2*, each one in a cavity, covered by tegumental fold. External cavity with microsensillum, subapical organite present between globular sensilla. Apical vesicle simple and globular (figure 47).

Postantennal organ with 14–15 vesicles (figure 46). Setae *c1* present on the head. Mouthparts relatively well-developed. Labrum with 2/534 setae.

Dorsal chaetotaxy presented in figure 45. Half tergite formula of setae *s*: 2, 2/1, 1, 1, 1, 1 in *m7* and *p4* position on thoracic tergites II and III, in *p4* position on the abdominal tergites I–IV, in *p2* position on abdominal tergite V. Setae *s* strongly lanceolate on third thoracic tergite (except *s*=*p4*), and on the second and third abdominal tergite, microsensilla *ms* on thorax II (figures 48–54). Ventral chaetotaxy as in figure 56; seta *m3* present on abdominal sternite II. Ventral tube with 4+4 distal setae.

Tibiotarsus I, II and III with 12 setae each, without tenent hair. Claw curved, toothless. Empodial appendage present (figure 55).

Anal spines curved. Ratio claw III : anal spines = 1 : 0·7.



Figs 45–56. *Willemia nepalensis* sp. n.: (45) dorsal chaetotaxy (scale 0·1 mm); (46) postantennal organ (scale 0·01 mm); (47) antennal segment II, III and IV (scale 0·01 mm); (48) seta *s* of thorax II (scale 0·01 mm); (49) seta *s* and microsensillum *ms* of thorax III (scale 0·01 mm); (50) seta *s* of abdomen I (scale 0·01 mm); (51) seta *s* of thorax II (scale 0·01 mm); (52) seta *s* of abdomen III (scale 0·01 mm); (53) seta *s* of abdomen IV (scale 0·01 mm); (54) seta *s* of abdomen V (scale 0·01 mm); (55) tibiotarsus III (scale 0·01 mm); (56) ventral abdominal chaetotaxy of the female (scale 0·1 mm).

Discussion

W. nepalensis is close to *Willemia annapurna*, from which it differs by number of vesicles in postantennal organ (19–21 in *W. annapurna*, 14–15 in *W. nepalensis*), by the number of setae on tibiotarsi I, II and III (11, 11, 10 in *W. annapurna*, 12, 12, 12 in *W. nepalensis*), and by the shape of setae *s* = *m7* on thoracic tergite III, which are subcylindrical and acuminate in *W. annapurna*, and lanceolate in *W. nepalensis*.

W. nepalensis is also close to *W. delamarei* from which it can be distinguished by number of vesicles in postantennal organ (8–12 in *W. delamarei*, 14–15 in *W. nepalensis*) and the shape of setae *s* = *m7* on thoracic tergite III, which are more strongly lanceolate in *W. nepalensis*.

Etymology

The species is named after Nepal, the country in which it was found.

Willemia wandae Tamura, 1997

(Table 1)

Material

China, Yunnan Province, Mengla, Menglum National Nature Forest Reserve, limestone-rich soil in tropical rain forest, 30.x.1992, H. Tamura and L. Zhao, paratype female; Thailand, Chiang Mai Province, Ban Tham Chiang Dao, forest on limestone, in rotten wood. 27.xii.1980, L. Deharveng and A. Bedos (MNHN) two females; Chiang Mai Province, Ban On Luoi near Tham Muang On Cave, forest on limestone, bamboo litter, 20.vii.1985, L. Deharveng and A. Bedos, three juvenile specimens; Nepal, Annapurna massif, Gokarna royal forest, Schima Wallichü, in deep humus, 1450 m, 13.x.1977, L. Deharveng, five specimens; Nepal, Annapurna massif, Siwalik, superior tropical forest with Shorea robusta and Terminalia tomentosa, in humus and litter, 660 m, 18.x.1977, L. Deharveng, one specimen.

Remarks

Length of specimens from Thailand: 0·44–0·47 mm (0·34–0·42 mm in Tamura and Zhao, 1997). Antennal segment IV with four thick sensilla (*e1*, *e2*, *i1* and *d*), shorter than ordinary setae; two large globular sensilla *e3* and *i2*, each one in a cavity, covered by tegumental fold, external cavity with a microsensillum, subapical organite present, apical vesicule simple and globular. Labrum with 2/534 setae, not as in the original description. Setae *c1* absent of the head.

Dorsal chaetotaxy: thoracic tergite II and III without setae *a6*. Ventral chaetotaxy without setae *a3* on abdominal sternite II and IV.

Tibiotarsus I, II and III all with 11 setae (not as in original description 10, 10, 10) without tenent hair.

Ratio claw III : anal spines = 1 : 1·3 material from Thailand (Tamura and Zhao (1997) = 1 : 1·2).

Willemia neocaledonica Weiner, 1991

(Table 1)

Material

New Caledonia, HOLOTYPE (♀): Lake 'en Huit', turf of Cyperaceae 4.iii.1986, J. Boudinot (MNHN), PARATYPE: the same data as holotype (ISEA); Rivière Bleue, humid forest on alluvion, A. and S. Tillier, three specimens; Rivière Blanche, litter in maquis, 7.iv.1986, J. Boudinot, two specimens. Thailand, Phangnga Province:

Phangnga, Ko Panak Is., soil under litter; 21.vii.1987, L. Deharveng and A. Bedos, one specimen.

Remarks

The original description made by Weiner in 1991 had to be completed with the following characters: postantennal organ with 10–15 vesicles, setae *a3* on abdominal sternite II absent, setae *a3* on abdominal sternite IV present, labrum with 2/534 setae.

Key to species *Willemia buddenbrocki*-group

1 Abdominal tergite V with setae *s* in the position of *p2*, 3 + 3 setae on thoracic tergite I . . . 2
– Abdominal tergite V with setae *s* in the position of *p3*, 2 + 2 setae on thoracic tergite I, curved and crenellated setae, *m1* absent on the fourth abdominal sternite . . . *W. nadchatrami* Yosii, 1959

2 Anal spines absent, apical vesicle absent . . . 3
– Anal spines present, apical vesicle present . . . 4

3 Antennal segment IV with ordinary setae, without lanceolate setae, postantennal organ with 18–20 vesicles . . . *W. setonychia* Prabhoo, 1971
– Antennal segment IV with ordinary setae and two lanceolate setae, postantennal organ with 15–17 vesicles . . . *W. deharvengi* sp. n.

4 Abdominal tergite IV and V with setae *s* subcylindrical and acuminate . . . 5
– Abdominal tergite IV and V with setae *s* lanceolate, postantennal organ with 8–12 vesicles . . . *W. delamarei* Prabhoo, 1971

5 All tibiotarsi with 12 setae . . . 6
– Tibiotarsi I and II with 11 setae, tibiotarsi III with 11 or 10 setae . . . 8

6 Thoracic tergite III with setae $s = m7$ subcylindrical and acuminate, antennal segment IV with two or four subcylindrical sensilla clearly distinct from normal setae . . . 7
– Thoracic tergite III with setae $s = m7$ lanceolate, antennal segment IV with four subcylindrical sensilla hardly distinguishable from normal setae . *W. nepalensis* sp. n.

7 Antennal segment IV with two subcylindrical sensilla, postantennal organ with 7–10 vesicles . . . *W. brevispina* Hüther, 1962
– Antennal segment IV with four subcylindrical sensilla, postantennal organ with 10–15 vesicles . . . *W. neocaledonica* Weiner, 1991

8 Postantennal organ with 12–14 vesicles, setae *c1* absent on head . . . 9
– Postantennal organ with about 20 vesicles, setae *c1* present on head *W. annapurna* sp. n.

9 Setae *a3* present on the second and fourth abdominal sternites, setae $s = m7$ on thoracic tergite III subcylindrical . . . *W. buddenbrocki* Hüther, 1959
– Seta *a3* absent on the second and fourth abdominal sternite, setae $s = m7$ on thoracic tergite III lanceolate . . . *W. wandae* Tamura, 1997

Cladistic analysis

Choice of the taxa

The ten species of *W. buddenbrocki*-group form the ingroup. An outgroup polarises the characters and tests monophyly. For the outgroup we found the following species: *W. anophthalma* Börner, 1901, *W. intermedia* Mills, 1934, *W. arenicola* Palacios-Vargas and Vazquez, 1989 and *W. meybholae* Palacios-Vargas, 1987 according to the cladogram obtained with all species of the genus (D'Haese *in litt.*). Therefore 14 species of the genus *Willemia* were analysed in our work.

Character states

We analysed 26 characters out of 50 studied. Autapomorphies, polymorphic characters, and ambiguous characters were eliminated so that significant and stable characters could be kept.

Multistate characters were treated unordered.

The matrix of characters is given in table 2.

Question marks represent a polymorphic, an inapplicable, or unknown character.

0. Apical vesical small (0), large (1).
1. Sensilla *e1* of antennal segment IV subcylindrical (0), globular (1), absent (2).
2. Sensilla *e2* of antennal segment IV subcylindrical (0), globular (1).
3. Sensilla *e3* of antennal segment IV subcylindrical (0), globular (1), globular in cavity (2).
4. Sensilla *d* of antennal segment IV subcylindrical (0), absent (1).
5. Sensilla *i1* of antennal segment IV subcylindrical (0), absent (1).
6. Sensilla *i2* of antennal segment IV subcylindrical (0), globular (1), globular in cavity (2).
7. Second antennal segment with 12 setae (0), 11 setae (1).
8. First antennal segment with seven setae (0), six setae (1).
9. Labral chaetotaxy of the second row with five setae (0), three setae (1).
10. Seta *a0* on the head present (0), absent (1).
11. Setae *c1* on the head present (0), absent (1).
12. Postantennal organ with 4–6 vesicles (0), 7–10 vesicles (1), >10 vesicles (2).
13. On the third thoracic tergite, setae *a2* present (0), absent (1).
14. On the third thoracic tergite, setae *m3* present (0), absent (1).
15. Tibiotarsi I and II with 17 setae (0), 12 (1) or 11 (2).
16. Tibiotarsus III with 16 setae (0), 12 (1), 11 or 10 (2).
17. On third thoracic tergite, setae *s* in *m7* position subcylindrical and acuminate (0), lanceolate (1).

Table 2. Matrix of states of the 26 characters in the 14 species.

	Characters					
			11111	11111	22222	2
Taxa	01234	56789	01234	56789	01234	5
annapurna	00020	02111	10201	22010	00110	0
anophthalma	00000	00000	00000	00010	00000	0
arenicola	11111	1111?	10?10	12000	01110	0
brevispina	02021	02111	11101	11010	00111	0
buddenbrocki	00020	02111	11201	22010	00110	0
deharvengi	20020	02111	10201	12111	10110	1
delamarei	00020	02???	10?01	??111	1011?	0
intermedia	02000	00000	00000	00010	00000	0
meybholae	11111	11111	10210	12000	01110	1
nadchatrami	00020	02111	11101	11000	00111	0
neocaledonica	00020	02111	11201	11010	00111	0
nepalensis	00020	02111	10201	11110	00110	0
setonychia	20020	02???	102??	??111	1011?	1
wandae	00020	02111	11201	22110	00111	0

18. On second and third abdominal tergite, setae *s* subcylindrical and acuminate (0), lanceolate (1).
19. On fourth abdominal tergite, setae *s* subcylindrical and acuminate (0), lanceolate (1).
20. On fifth abdominal tergite, setae *s* subcylindrical and acuminate (0), lanceolate (1).
21. On abdominal I, II and III tergite, setae *a2* present (0), absent (1).
22. On fourth abdominal tergite, setae *m1* present (0), absent (1).
23. On fourth abdominal tergite, setae *m3* present (0), absent (1).
24. On second abdominal sternite, setae *a3* present (0), absent (1).
25. Anal spines present (0), absent (1).

Results and discussion

Phylogenetic analysis was performed under Hennig86 (Farris, 1988). The algorithm ie (implicit enumeration) was used to build tree(s), using Wagner parsimony. One tree of 40 steps was generated, for which the consistency and retention indices are ci = 82 and ri = 86 (figure 57).

Monophyly of the W. buddenbrocki-group

The *W. buddenbrocki*-group is monophyletic and forms a clade clearly distinctive from the other species. Monophyly is supported by the following synapomorphies:

e3 and *i2* sensilla of the fourth antennal segment are large, placed in cavity and covered in part by tegumental fold (characters 3: 2, 6: 2);

third thoracic tergite without *m3* setae (character 14: 1);

In this clade, *s* lanceolate setae at the fourth and fifth abdominal tergite are the

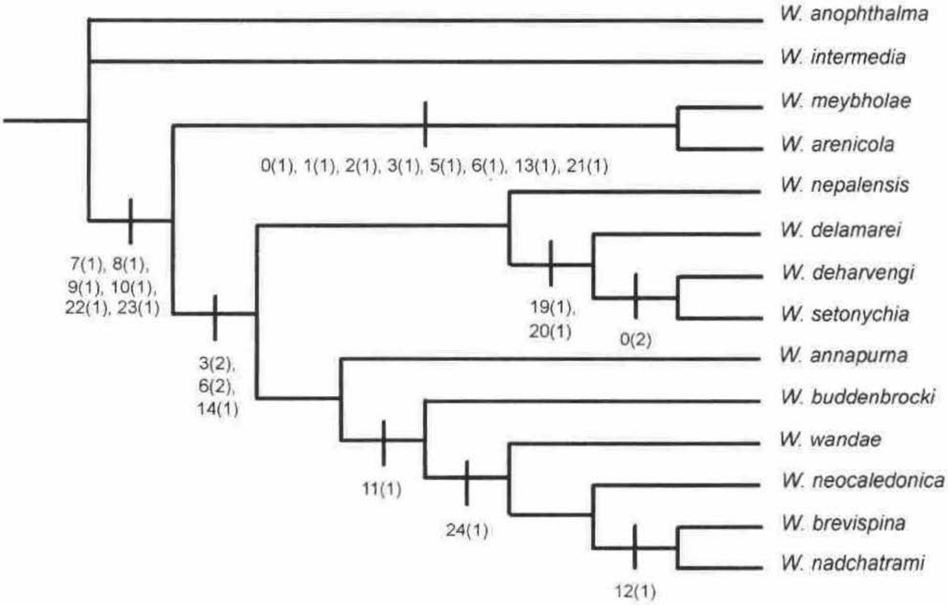


FIG. 57. Cladogram obtained with the 'ie' comand of Hennig86 on data shown in table 2. 14 taxa, 26 characters, ci = 82, ri = 86, length = 40 steps, 1 tree.

synapomorphies of the clade formed by *W. delamarei*, *W. setonychia* and *W. deharvengi* (characters 19: 1 and 20: 1). The lack of apical vesicle is the synapomorphy of *W. setonychia* and *W. deharvengi* (characters 0: 2), they also share absence of anal spines.

W. buddenbrocki, *W. annapurna* and *W. wandae* make a paraphyletic group characterized by 11 setae on tibiotarsi I, II and 11 or 10 setae on tibiotarsus III (characters 15: 2 and 16: 2).

The lack of the setae *c1* on the head is the synapomorphy of the species *W. buddenbrocki*, *W. wandae*, *W. neocaldonica*, *W. brevispina* and *W. nadchatrami* (character 11: 1). Inside this clade, *W. wandae*, *W. neocaledonica*, *W. brevispina* and *W. nadchatrami* don't have setae *a3* on the second abdominal sternite (character 24: 1) and *W. brevispina* and *W. nadchatrami* have postantennal organ with 7–10 vesicles (12: 1).

Characters' transformation

As a general rule, subcylindrical setae *s* on thoracique tergites II and III, and abdominal tergites I–V represent a primitive state whereas the other shapes of setae *s* are derived states.

A complete chaetotaxy is a plesiomorphic state whereas, setae disappearance is an apomorphic state. We can see it particularly in the number of setae of the tibiotarsi, of antennal segments I and II, and thoracic tergite I. Sensilla *e3* and *i2* on the fourth antennal segment are primitively subcylindrical, then globular. In the most advanced state the mentioned sensilla are large and situated inside a kind of cavity and covered by a tegumentary fold.

W. nadchatrami is one of the most specialized and at the same time most peculiar species (crenated setae, shape of *e3* and *i2* setae). The particular morphology of this species could be related to its way of life: it is the only species in the group described, that lives on guano in caves.

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